## THE CHROMOSOMES OF TRAGOPOGON ${ }^{1}$

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Although interspecific hybrids have been known in the Old World genus Tragopogon (Compositae) for nearly two centuries, the realization that this genus furnishes unusually favorable materials for the study of evolutionary relationships has been slow to develop. In his classic pioneer study, Winge (1938) worked out some of the cytogenetic relationships between $T$. porrifolius and T. pratensis, and Ownbey (1950) has given an account of the recent origin of two amphiploid species through natural hybridization. The present authors (1953) have summarized the evidence for cytoplasmic inheritance in the genus and have reported briefly on a number of interspecific crosses yet to be considered in detail. This paper records the karyotypes of fifty collections representing eight species of the genus assembled in our laboratory from various sources.

Among previous studies, only that of Winge (1938) considers in any detail the morphology of the somatic chromosomes of any species. Winge found Tragopogon porrifolius and T. pratensis each to have six pairs of chromosomes differing between the species significantly with respect to over-all length of some of the corresponding members of the two sets, the position of the primary constriction, and the presence or absence of a second satellite. Aside from the work of Winge, chromosome numbers of five species have been reported by Poddubnaja-Arnoldi et al. (1935) as follows: T. brevirostris, $2 n=12 ; T$. cupani, $2 n=24$; T. major (dubius), $2 n=12 ; T$. marginatus, $2 n=12$; and $T$. porrifolius, $2 n=12$. From meiotic studies, Ownbey (1950) confirmed the above reports for $T$. dubius, T. porrifolius, and T. pratensis, and added $T$. mirus $(2 n=24)$ and $T$. miscellus $(2 n=24)$ to the list of species which have been studied.

Materials and Methods.-The sources of the materials used in these studies are given by species in the following table. We are grateful for the kind assistance of the collectors and correspondents mentioned. Except when otherwise indicated, the localities are in North America where Tragopogon has been introduced in post-Columbian time.

[^0]| Species | Garde Numbe | Race Name | $2 n$ | Fig. | Source |
| :---: | :---: | :---: | :---: | :---: | :---: |
| T. dubius | 1 | Pullman | 12 | 1 | Washington. Whitman Co.: 1 mi . s. of Pullman, M. Ownbey |
| T. dubius | 16 | Colton | 12 | 2 | Washington. Whitman Co.: w. of Colton, M. Ownbey |
| T. dubius | 18 | Rowena | 12 | 3 | South Dakota. Minnehaha Co.: $21 / 2 \mathrm{mi}$. w. of Rowena, M. Ownbey |
| T. dubius | 19 | Douglas | 12 | 4 | Washington. Douglas Co.: near Douglas, M. Ownbey |
| T. dubius | 20 | Hulett | 12 | 5 | Wyoming. Crook Co.: 7 mi n. w. of Hulett, M. Ownbey |
| T. dubius | 21 | Dardanelles | 12 | 6 | Washington. Chelan Co.: near Dardanelles, M. Ownbey |
| T. dubius | 22 | Rugby | 12 | 7 | North Dakota. Pierce Co.: 1 mi . s. w. of Rugby, M. Ownbey |
| T. dubius | 23 | Reliance | 12 | 8 | South Dakota. Lyman Co.: 3 mi . s. w. of Reliance, M. Ownbey |
| T. dubius | 24 | Vancouver | 12 | 9 | British Columbia. Vancouver Island: about $20 \mathrm{mi} . \mathrm{n}$. of Victoria, M. Ownbey |
| T. dubius | 28 | Twin Falls | 12 | 10 | Idaho. Twin Falls Co.: e. of Twin Falls, M. Ownbey |
| T. dubius | 35 | Bloomington | 12 | 11 | Indiana. Monroe Co.: 2 mi . s . of Bloomington, D. M. Smith |
| T. dubius | 36 | Fortville | 12 | 12 | Indiana. Hancock Co.: 1.4 mi . s. w. of Fortville, D. M. Smith \& C.B. Heiser |
| T. dubius | 37 | Jefferson | 12 | 13 | Indiana. Jefferson Co.: near junction, highways 3 and $256, D . M$. Smith |
| T. dubius | 43 | Aurora | 12 | 14 | Kansas. Cloud Co.: Aurora, Rev. S. V. Fraser |
| T. dubius | 45 | Blewett | 12 | 15 | Washington. Kittitas Co.: s. approach to Blewett Pass, $D . L$. Goodwin |
| T. dubius | 47 | Guelph | 12 | 16 | Ontario. Guelph, F. H. Montgomery |
| T. dubius | 61 | Eugene | 12 | 17 | Oregon. Lane Co.: 4 mi . n . of Eugene, M. Ownbey \& S. J. Preece, $J r$. |
| T. cupani | 68 | Catania | 12 | 18 | Italy. Sicily: Catania, Dr. G. Rodio |
| T. cupani | 70 | Florence I | 12 | 19 | Italy. Seeds mixed with those of T. porrifolius from the Instituto Botanico della Universitá di Firenze, Dr. A. Chiarugi |
| T. cupani | 72 | Florence II | 12 | 20 | Italy. Seeds mixed with those of T. pratensis from the Instituto Botanico della Universitá di Firenze, Dr. A. Chiarugi |
| T. porrifolius | S 2 | Pullman | 12 | 21 | Washington. Whitman Co.: Pullman, M. Ownbey |
| T. porrifolius | S 25 | Victoria | 12 | 22 | British Columbia. Vancouver Island: Victoria, M. Ownbey |
| T. porrifolius | s 27 | Twin Falls | 12 | 23 | Idaho. Twin Falls Co.: e. of Twin Falls, M. Ownbey |


| Species | Gard Numb | Race Name | $2 n$ | Fig. | Source |
| :---: | :---: | :---: | :---: | :---: | :---: |
| T. porrifolius | 34 | Madison | 12 | 24 | Indiana. Madison Co.: s. w. of junction, highways 67 and 232, C. B. Heiser \& D. M. Smith |
| T. porrifolius | 44 | Grangeville | 12 | 25 | Idaho. Idaho Co.: Grangeville, M. Ownbey |
| T. porrifolius | 50 | Guelph | 12 | 26 | Ontario. Guelph, F. H. Montgomery |
| T. porrifolius | 62 | Eugene | 12 | 27 | Oregon. Lane Co.: $4 \mathrm{mi} . \mathrm{n}$. of Eugene, M. Ownbey \& S. J. Preece, $J r$. |
| T. porrifolius | 63 | Weed | 12 | 28 | California. Siskiyou Co.: $4 \mathrm{mi} . \mathrm{n}$. of Weed, M. Ownbey \& S. J. Preece, $J r$. |
| T. porrifolius | 65 | Ferry-Morse | 12 | 29 | Distributed by Ferry-Morse Seed Company as "Mammoth Sandwich Island Salsify" |
| T. porrifolius | 66 | Corvallis | 12 | 30 | Oregon. Benton Co.: Corvallis, M. Ownbey \& S. J. Preece, Jr. |
| T. pratensis | 3 | Moscow | 12 | 31 | Idaho. Latah Co.: Moscow, M. Ownbey |
| T. pratensis | 26 | Seattle | 12 | 32 | Washington. King Co.: 85th Street, near Aurora, Seattle, $M$. Ownbey |
| T. pratensis | 31 | Michelbach | 12 | 33 | Germany. Württemburg: Michelbach an der Bilz, Dr. H. Scheerer |
| T. pratensis | 32 | Uppsala | 12 | 34 | Sweden. Uppsala, H. J. Brodie |
| T. pratensis | 33 | Madison | 12 | 35 | Indiana. Madison Co.: s. w. of junction, highways 67 and 232, C. B. Heiser \& D. M. Smith |
| T. pratensis | 48 | Guelph | 12 | 36 | Ontario. Guelph, F. H. Montgomery |
| T. pratensis | 49 | Waterdown | 12 | 37 | Ontario. Near Waterdown, F. H. Montgomery |
| T. pratensis | 64 | Mt. Shasta | 12 | 38 | California. Siskiyou Co.: Mt. Shasta (city), M. Ownbey \& S. J. Preece, Jr. |
| T. pratensis ${ }^{2}$ | 71 | Florence | 12 | 39 | Italy. Seeds from Instituto Botanico della Universitá di Firenze, Dr. A. Chiarugi |
| T. longirostris | 46 | Jerusalem | 12 | 40 | Israel. Jerusalem, Dr. N. Feinbrun |
| T. orientalis | 77 | Michelbach | 12 | 41 | Germany. Württemburg: seeds mixed with those of $T$. pratensis, Michelbach a. d. Bilz, Dr. H. Scheerer |
| T. orientalis | 59 | Graz | 12 | 42 | Austria. Botanischer Garten der Universität, Graz, Dr. F. Widder |
| T. orientalis | 60 | Königstuhl | 12 | 43 | Austria. Ostalpen, Norische Alpen, Voralpenwiesen zwischen Kleinem und Grossen Königstuhl, Dr. F. Widder |
| T. orientalis | 67 | Glashütten | 12 | 44 | Austria. Lavanttaler Alpen, Koralpe, Wiesen unter Glashütten, $D r$. F. Widder |

${ }^{2}$ Of the collections listed, this one alone has not flowered, and the original determination has been accepted without further verification. All other collections are represented by voucher specimens preserved in the Herbarium of the State College of Washington.

| Species | Garden Number | Race Name | $2 n$ | Fig. |  | Source |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| T. mirus | 4 | Pullman | 24 | 45 | Washington. man, M. Ownbe | Whitman Co.: Pulley |
| T. mirus | 5 | Palouse | 24 | 46 | Washington. louse, M. Ownb | Whitman Co.: Paby |
| T. mirus | 29 | Tekoa | 24 | 47 | Washington. koa, M. Ownbey | ${ }_{y}$ Whitman Co.: Te- |
| T. miscellus | 6 | Moscow I | 24 | 48 | Idsho. Latah Ownbey | Co.: Moscow, M. |
| T. miscellus | 7 | Moscow II | 24 | 49 | Idaho. Latah Ownbey | Co.: Moscow, M. |
| T. miscellus | 30 | Moscow III | 24 | 50 | Ірано. Latah Ownbey | Co.: Moscow, M. |

The seeds were germinated on moist filter paper in Petri dishes at $15^{\circ} \mathrm{C}$., and the young seedlings transferred to soil in pots when the primary root appeared. They were then grown at prevailing temperatures (in August) until ready to transplant to the garden at an age of about three weeks. The lowered temperature is necessary for the initiation of germination, but after growth is started higher temperatures produce no ill effects. At an age of about three weeks, the potted plants were placed in a refrigerator and chilled over night at just above $0^{\circ} \mathrm{C}$. This treatment shortens and straightens the chromosomes which, when fixed without chilling, are long and tangled. Maximum contraction, however, is not desirable as often it obscures such morphological features as satellites and secondary constrictions, although enhancing the primary constriction. Fixation was in Belling's modified Navashin's fluid, after which the root tips were embedded in paraffin, sectioned at 15 microns, and stained with iodine-crystal violet. After careful study, one or more of the most representative plates from each collection were selected, and camera lucida drawings made at a magnification of 2700 diameters (reduced to $2000 \times$ in reproduction).

Observations.-The chromosome base number of Tragopogon, as previous studies have shown, is six, with the chromosome sets of the different species with much in common. There is considerable variation in the over-all length of the individual chromosomes of a set, most species clearly having three long and three short pairs. For convenience in discussion, the chromosomes of each set are lettered from A to F generally according to over-all length. Chromosomes assigned the same letter are not necessarily homologous in different species, but that appears


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Fig. 1-20. Chromosomes of Tragopogon.-Fig. 1-17. T. dubius $(2 n=12)$. -Fig. 18-20. T. cupani $(2 n=12) . \quad \times 2000 . \quad$ Additional explanation in text.
to be the usual situation. In general, the chromosome sets of different races of a single species resemble each other more closely than do those of races belonging to different species. There is more variation, however, between different races of a single species than has generally been supposed. The most usual intraspecific variation noted is found in the satellites, although there is some evidence that the relative lengths of the arms of a particular chromosome may vary within a species. The variation in the satellites is complicated by the fact that these structures may appear double (in tandem), single, or not at all in the same root tip or even in the same cell. Our studies, however, have been extensive enough to show clearly that the differences reported between races in these respects are probably real differences. Where the material is ample, it is possible to demonstrate these features even though they may not show clearly in every instance. What is said about satellites applies with even greater emphasis to secondary constrictions. In those races in which secondary constrictions occur, they can be seen with sufficient frequency that there is no question about their occurrence; in those races in which secondary constrictions are not reported, there has been adequate opportunity in most instances to observe them if they were there.

Tragopogon dubius.-Seventeen races of this species have been studied from localities scattered from Ontario and Indiana to the Pacific Ocean. All have twelve somatic chromosomes (fig. $1-17)$. There is considerable morphological and some chromosomal variation among the races. The chromosome set consists of three long and three short chromosomes. The longest chromosome "A" has very unequal arms and usually a single satellite. The second longest chromosome " $B$ " also has very unequal arms as does the third, "C." The short arm of the "B" chromosome is shorter than the short arm of the "C" chromosome. The three short chromosomes have submedian primary constrictions and are nearly indistinguishable. One of them, "D," is often of greater over-all length than the other two, and in one race (Colton, fig.2) its primary constriction did not appear to be quite submedian. The three short chromosomes are often characterized by terminal knobs set off by subterminal secondary constrictions. The total number of knobs is usually not clear, but
it appears that in at least some of the races all three of the short chromosomes have knobs at both ends. A similar knob occurs on the short arm of the "C" chromosome in most of the races. Somewhat longer segments are cut off by secondary constrictions on the long arm of the " A " chromosome in four races (Rowena, fig. 3; Vancouver, fig. 9; Twin Falls, fig. 10; Bloomington, fig. 11), on the long arm of the "B" chromosome in two races (Vancouver fig. 9; Twin Falls, fig. 10), and on the long arm of the "C" chromosome of two races (Vancouver, fig. 9; Jefferson, fig. 13). These constrictions are obscure and may have been overlooked in other races. A prominent secondary constriction in the middle of the long arm of the " $B$ " chromosome appears in one race (Blewett, fig. 15). This would not have been overlooked had it occurred elsewhere. Tandem satellites on the short arm of the "A" chromosome were found in two races (Douglas, fig. 4a; Hulett, fig. 5). In the former, one of the plants studied showed this feature clearly at times, but it could not be found in any of the material of a sister plant (this line has been selfed for two generations).

Tragopogon cupani.-All three of the collections of this species studied have twelve somatic chromosomes (fig. 18-20). Each chromosome set consists of three long and three short members, and the positions of the primary constrictions are the same as in T. dubius. There is some indication of a terminal knob on at least the " D " chromosome, but no other indication of a secondary constriction. In one of the collections (fig. 19), definite tandem satellites are evident on the short arm of the "A" chromosome. In the other two collections, only a single satellite could be discerned with certainty. The material, however, was not as ample as could have been desired, and in one of the latter collections there was some suggestion that the satellite might actually be two.

These observations do not agree with the previous report of $2 n=24$ in T. cupani (Poddubnaja-Arnoldi, et al., 1935), and that report must remain uncertain until it can be confirmed in material of certain identity. The identity of our material, also, is subject to further scrutiny.

Tragopogon porrifolius.-Ten collections of this species have been studied, nine from localities scattered from Indiana and


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Fig. 21-40. Chromosomes of Tragopogon.-Fig. 21-30. T. porrifolius $(2 n=12)$. -Fig. 31-39. T. pratensis $(2 n=12)$. -Fig. 40. T. longirostris $(2 n=12) . \times 2000$. Additional explanation in text.

Ontario to the Pacific Ocean, and one from cultivation. All have twelve somatic chromosomes (fig. 21-30). Among the races, there is considerable morphological and some chromosomal variation. The chromosome set consists of three long and three short chromosomes, but the longest short one is about as long as the shortest long one. In none of the chromosomes is the primary constriction strictly median, although in the shortest one it might be termed submedian. The four longest chromosomes have very unequal arms, and as in T. dubius the short arm of the " C " chromosome usually is longer than the short arm of the "B." The satellites are small and often difficult to find. There is reason to believe that both the "A" and "D" chromosomes are regularly with satellites, but both have not been found with satellites in every collection. Tandem satellites occur on the "A" chromosome in two collections (Guelph, fig. 26; Weed, fig. 28). It is perhaps significant that no satellite was found on the "D" chromosome in either of these collections. Secondary constrictions and terminal knobs are absent or obscure in T. porrifolius.

The above results agree closely with those of Winge (1938). Although he found no difference between the " B " and " C " chromosomes in his material, and he found the " F " chromosome to have a median primary constriction, it is possible to interpret some of our material in exactly the same way.

Tragopogon pratensis.-Nine collections of this species have been studied, six from localities scattered from Ontario and Indiana to the Pacific Ocean, and one each from Sweden, Germany, and Italy. All have twelve somatic chromosomes (fig. 31-39). The considerable morphological variation among the races may be correlated with chromosomal variation. The chromosome set consists of three long and three short chromosomes. The three long chromosomes have very unequal arms, with the short arm of the " C " chromosome longer than the short arm of the "B." Sometimes the "C" chromosome has a greater over-all length than the "B." The short chromosomes are of two types. In the " D " chromosome, the arms are unequal, but in the " E " usually and in the " $F$ " chromosomes, the primary constriction is submedian or nearly so. In two races (Mt. Shasta, fig. 38; Florence, fig. 39), the arms of the " $E$ " chromosome are unequal.

Secondary constrictions and knobs-although they occur-have not been found to be dependably characteristic of any race. A most conspicuous feature in five of the races (Moscow, fig. 31; Seattle, fig. 32; Madison, fig. 35; Mt. Shasta, fig. 38; Florence, fig. 39) is the presence of tandem satellites on the short arm of the " A " chromosome. In the four remaining races, the satellite on the "A" chromosome is single (Michelbach, fig. 33; Uppsala, fig. 34; Guelph, fig. 36; Waterdown, fig. 37). These four races may all belong to the taxon minor which different European botanists have assigned a rank varying all the way from forma to species. If this is true, however, the taxon minor will be very difficult to characterize morphologically, which is undoubtedly the reason for the uncertainty concerning its rank.

Winge's material (1938) belonged to the taxon minor and differed slightly from any race which we have studied. The "A" chromosome possessed a single satellite. The "B" chromosome was shorter than the "C," and only the "F" chromosome showed a submedian primary constriction. All of these features have been found in our material, but not in this combination. The basis for the report of $2 n=14$ in T. pratensis ssp. pratensis (Clapham, et al., 1952) is completely obscure.
Tragopogon longirostris.- Only a single race of this species has been available for study (Jerusalem, fig. 40). It has twelve somatic chromosomes, each set consisting of three long and three short ones. The three longest chromosomes have very unequal arms, and the short arm of the " B " is shorter than the short arm of the "C." A single satellite is found on the short arm of the "A," and a rather prominent knob is set off by a secondary constriction on the short arm of the "C." The longest of the short chromosomes "D" also has unequal arms, but the arms of the remaining two are subequal in length. Indistinct knobs occur on some of the short chromosomes.

Tragopogon orientalis.-This taxon is often considered to represent only a subspecies of T. pratensis to which it is undoubtedly closely related. Unlike the latter, however, our plants are selfsterile, leading us to the belief that two species are actually involved. Hybrids between the two are easily obtained, but they are highly sterile-about as much so as the $\mathrm{F}_{1}$ hybrid between $T$. pratensis and T. porrifolius. Self-sterility is dominant in the $\mathrm{F}_{1}$.


Fig. 41-50. Chromosomes of Tragopogon.-Fig. 41-44. T. orientalis $(2 n=12)$.-Fig. 45-47. T. mirus $(2 n=24)$.-Fig. 48-50. T. miscellus $(2 n=24) . \times 2000$. Additional explanation in text.

Four races of this species have been studied, all from Germany and Austria. All have twelve somatic chromosomes (Fig. 41-44), and the chromosome set consists of three long and three short members. The three long chromosomes have very unequal arms, with the short arm of the " B " shorter than the short arm of the "C." In two of the races (Graz, fig. 42; Königstuhl, fig. 43), the satellite on the short arm of the " A " chromosome is solitary. In the other two races (Michelbach, fig. 41; Glashütten, fig. 44), two satellites occur in tandem in this position. The "D" chromosome in all races has unequal arms, and in one, Graz, shows a secondary constriction in the middle of the long arm. In the
remaining two chromosomes, the primary constriction is median or submedian in position.

From the above it is evident that there are no clear chromosomal distinctions between $T$. pratensis and $T$. orientalis, an observation which is in accord with the idea based on external morphology that the two are closely related. However, if the self fertility of the first, the self sterility of the second, and the sterility of the hybrids between them are considered to be valid differences, the two are clearly distinct species.

Tragopogon mirus.-In addition to the two localities previously reported (Ownbey, 1950), this tetraploid species is now known from Tekoa, Washington. The newly discovered colony is the most extensive one yet found, and the several thousand individuals comprising it are, on the average, significantly more fertile than are those of the other two colonies. From morphological and distributional data, it seems clear that the three colonies represent three independent instances of the origin of T. mirus. The chromosomal and fertility data also support this conclusion.

Inasmuch as the chromosome sets of the diploid T. dubius and T. porrifolius differ in a number of respects, the chromosomes of $T$. mirus should provide exceedingly critical evidence in support of its origin from these species through hybridization and amphiploidy. This evidence has been obtained. Where the chromosomes of the diploid species differ, a pair of each type is found in the tetraploid; where the diploid chromosomes are alike, four of a kind are present. Stronger evidence supporting the amphiploid origin of $T$. mirus can be obtained only by its artificial synthesis. Because of the larger number of chromosomes present in the tetraploid, it has not been possible to show all of the evidence in the single metaphase plate of each collection selected for illustration. Most complete is figure 47 (Tekoa), in which all six satellited chromosomes have been identified. It will be recalled, however, that in the Pullman race of $T$. porrifolius, satellites are difficult to find on the "A" chromosomes (they are so rare that one could not be found on a metaphase plate suitable for illustration). It is not surprising, therefore, that they were not found with any greater frequency on the " A " porrifolius chromosomes in the tetraploid derived from the Pullman race (fig. 45). The same is true of Palouse mirus (fig. 46), and it may
be assumed that T. porrifolius in Palouse (which was not studied) is like the Pullman race in this respect. The satellites which are shown on the " A " chromosomes of Palouse mirus are sometimes clearly in tandem (fig. 46). These chromosomes must have come from a race of T. dubius in which tandem satellites occur. This means that the race of $T$. dubius entering into the formation of Palouse mirus must have been a different one than the one entering into the formation of Pullman mirus. Similarly, the presence of single satellites on all four "A" chromosomes in Tekoa mirus indicates that the race of T. porrifolius entering into its makeup was different from that entering into either of the other races of $T$. mirus. This evidence is in strong support of the independent origin of the three races of T. mirus.

Tragopogon miscellus.- In addition to the two Moscow localities previously reported (Ownbey, 1950), this tetraploid species was found at a third Moscow locality ${ }^{3}$ at which it has now been destroyed by the building of a house and the planting of a lawn (the race, however, brought into the garden, has not been lost). This race appears to represent the reciprocal of the ones first discovered (Ownbey \& McCollum, 1953), and like Tekoa mirus is significantly more fertile, on the average, than either of the other two races. Its independent origin seems clear.

As in the case of the previous tetraploid, the chromosome sets of the two diploid species, T. dubius and T. pratensis, from which $T$. miscellus is believed to have originated, differ in a number of respects. The "A" chromosome of T. pratensis (Moscow race) has tandem satellites; that of $T$. dubius usually has a single satellite. The "D" chromosome of T. pratensis has unequal arms; that of $T$. dubius has a submedian primary constriction. T. miscellus (fig. 48-50) conforms to expectations and has two chromosomes of each type, the remaining chromosomes being in fours. Thus the chromosomal evidence provides strong support for the origin of T. miscellus from T. dubius and T. pratensis through hybridization and amphiploidy.

DISCUSSION.-Evolution in the genus Tragopogon evidently has been preceded or accompanied by extensive repatterning

[^1]of the chromosomes, which has resulted in chromosomal races within a species as well as chromosomal differences between the species. This situation is by no means unique; an even more extreme example, inasmuch as different chromosome base numbers also are found, is presented by the genus Holocarpha (Clausen, 1951), and indications are found in numerous genera that this is an important mechanism of speciation. It is to be expected, of course, that any repatterning of the chromosomes, particularly that which involves the translocation of a segment from one chromosome to another, will result in the establishment of at least a partial sterility barrier between races so differentiated. Furthermore, subsequent repatterning will build a cumulatively higher and higher barrier leading to the complete or nearly complete isolation commonly characteristic of species, perhaps unaccompanied by any other kind of evolutionary divergence. This possibility has been realized in Holocarpha, where interracial hybrids, when they can be obtained, are usually nearly or completely sterile, but the parental races are so much alike in external morphology that few would think of setting them up as distinct species on the basis of genetic isolation alone. Clearly, chromosome rearrangements, like incompatability genes, are merely the blocks from which barriers to gene interchange are built. It is not the height of the barrier nor the kind of a barrier which is important from an evolutionary standpoint, but the divergence which it permits.

The importance of hybridization in hastening the erection of barriers to interbreeding is not yet clear. Certainly in the initial stages, hybridization between races homozygous for different chromosome rearrangements, in a frequently self-pollinated genus like Tragopogon, could result in the production of a race homozygous for both. Should this in itself confer a selective advantage on the race so endowed, or should a favorable mutation occur in it and not in the parental races, any further strengthening of the barrier to gene exchange would be of great selective value. It is possible, of course, that the repatterning of the chromosomes in Tragopogon species is not a primary phenomenon, but is the result of hybridization between existing species. A situation of this kind would be of exceedingly great evolutionary interest and significance.

## SUMMARY

The somatic chromosomes of fifty races representing eight species of the genus Tragopogon are described and figured. Although there is much in common between the chromosome sets of the different species, most species can be recognized by the morphology of the chromosomes. Even within a single species, however, considerable chromosomal variability occurs among different races. The chromosome number was found to be $2 n=12$ in the following species: T. cupani (3 races), T. dubius (17 races), T. longirostris (1 race), T. orientalis (4 races), T. porrifolius ( 10 races), and T. pratensis ( 9 races). In T. mirus and T. miscellus, it is $2 n=24$. The origin of $T$. mirus through hybridization and amphiploidy between $T$. dubius and T. porrifolius is confirmed by its chromosome morphology, as is the origin of $T$. miscellus through hybridization and amphiploidy between $T$. dubius and $T$. pratensis. The independent origin of the three known races of $T$. mirus also is confirmed by chromosomal evidence.-state college of washington, pullman.

## LITERATURE CITED

Clapham, A. R., T. G. Tutin, and E. F. Warburg. 1952. Flora of the British Isles. Cambridge, Cambridge Univ. Press.
Clausen, J. 1951. Stages in the evolution of plant species. Ithaca, Cornell Univ. Press.
Ownbey, M. 1950. Natural hybridization and amphiploidy in the genus Tragopogon. Amer. Jour. Bot. 37: 487-499, 1 plate.
Ownbey, M., and G. D. McCollum. 1953. Cytoplasmic inheritance and reciprocal amphiploidy in Tragopogon. Amer. Jour. Bot. 40: In press.
Poddubnaja-arnoldi, W., N. Steschina, und A. Sosnovetz. 1935. Der Charakter und die Ursachen der Sterilität bei Scorzonera tausaghys Lipsch. et Bosse. Beih. Bot. Centralblatt 53A: 309-339.
Winge, Ö. 1938. Inheritance of species characters in Tragopogon. A cytogenetic investigation. Compt. Rend. Trav. Lab. Carlsberg, Série Physiol. 22: 155-196, 2 plates.

A New Species of Carex (Section Phyllostachyae) from Oкlahoma.-In the spring of 1951 a peculiar species of Carex was collected by the author in the Ouachita Mountains of southeastern Oklahoma. Although too immature for determination, it obviously belonged to the section Phyllostachyae since the lower pistillate bracts were broad and leaflike, exceeding the inflorescence, and the staminate scales of the single androgynous


[^0]:    ${ }^{1}$ This investigation was supported in part by funds provided for biological and medical research by State of Washington Initiative Measure No. 171.

[^1]:    : In June, 1953, T. miscellus was found growing at two additional well-separated localities near Sheridan, Wyoming. As at the Moscow localities, T. dubius, T. pratensis, and the $\mathrm{F}_{1}$ hybrid between them were found with the amphiploid.

